CONTRIBUTORY THOUGHTS ON FORM, FUNCTION, HABITAT AND CLASSIFICATION OF HYDROIDS AND HYDROMEDUSAE

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Because of the manifold variations of structure and life-history among the Hydroida and of the way in which, historically, our knowledge has been gradually acquired, and because of the tendency among many workers to specialize in either hydroids or medusae, the fullest advancement of the science has been hampered by two systems of classification and nomenclature, one for hydroids and another for hydromedusae. The need for rectifying this anomalous dual system has long been recognized, but attainment of a unified system has been delayed by lack of knowledge of the life-histories of numerous species. Many life-histories had been worked out by pioneer naturalists of the nineteenth century, but until recent decades there continued to exist large gaps in knowledge of relationships between medusae and hydroids, even in the relatively well-known fauna of Europe. In the years 1935–1940 a special effort was made by F.S. RUSSELL and W.J. REES at the Plymouth Laboratory (RUSSELL, 1953: Introduction) to discover and rear the unknown hydroids of British medusae, and many gaps were closed. During the past 20 years or so the life-histories of many further European species have been successfully worked out, particularly by Dr Bernhard WERNER at Hamburg, Drs Marta VANNUCCI, Anita BRINCKMANN-VOSS and Kay PETERSEN at Naples, and the present author at Millport and Oban. It is an especial pleasure at this meeting to refer to the fine studies on hydroids and medusae carried out in Japan, and I wish to pay tribute to Professor Tohru UCHIDA, Zen NAGAO and others. Very much remains to be done in various parts of the world on whole life-histories. Studies of hydroids or medusae alone, though often unavoidable, are insufficient to lead to a material advance of our knowledge of the Hydroida.

There has been long-continued interest in the evolution of the Hydrozoa and in their phylogenies, and many attempts have been made to construct a 'natural classification' based on presumed phylogenetic relationships. Many theories have in the past been advanced to explain the origin and development of the complicated and varied life-histories. These theories have centred especially around the nature of the two phases, the hydroid and the medusa, and there has been much discussion of the 'alternation of generations' or 'metagenesis'. In the context of zoological thought of the nineteenth century and of the gradual and often piecemeal growth of knowledge this long discussion, often with a philosophical flavour, was inevitable. I shall not discuss the various theories of the evolution of the Hydroida. To my mind, with the benefit of hindsight, it seems that the arguments and the theorising have been unduly

prolonged and to a large extent unnecessary and that in reality the varied life-histories in the Hydroida are all referable to a basic life-cycle essentially similar to life-cycles with larval development found in many other groups of animals. I am doubtful of the usefulness of arguing whether, in the history of the group, the medusa preceded the polyp or the polyp was ancestral to the medusa. I consider that extremely early a life-cycle was established involving development from the fertilized ovum to the blastula, thence to a ciliated gastrula (the 'planula'), thence to a tentacled polypoid larva, and finally to a muscular swimming adult. These stages in present-day life-histories should not, to my mind, be construed as indicating anything of the evolutionary history of the group. Haeckelian attempts to relate ontogenetic development to the phylogenetic history of the Hydroida seem to me of very doubtful validity and to have caused unnecessary difficulties. I am aware that I am in company with a majority of modern workers in regarding the hydroid stage as a larval stage in the life-cycle.

If it be accepted that basic to the Hydroida there is a life-cycle involving development from the ovum through blastula and gastrula stages to a tentaculate polypoid larva and thence to a muscular swimming adult, all the variant life-histories of different species can readily be explained as specializations and modifications to meet ecological and physiological needs.

Let us first consider the gastrula stage. Although a ciliated free-swimming gastrula (the 'planula') is commonly present in life-cycles, this stage is omitted or much modified in some species. For example, in the medusa species *Hybocodon prolifer* L. AGASSIZ the fertilized ova, which are few, are retained on the gonad of the medusa, where they undergo cleavage and become amoeboid, developing at the expense of other cells. Each develops into a young tentaculate polyp (an 'actinula') while still in the umbrellar cavity of the medusa (BROWNE, 1895, p. 254: as *Amphicodon fritillaria*; HARGITT, C.W., 1905, p. 33; MÜLLER, 1908; HARGITT, G.T., 1917; KARMP, 1926, pp. 36–38; UCHIDA, 1927, pp. 162–4; UCHIDA and NAGAO, 1960). After release from the medusa the actinula, which has only a brief planktonic phase, elongates and changes into a typical hydroid polyp with a hydrocaulus and with a hydrorhiza enclosed in perisarc, by which it becomes attached to the bottom. The omission of the free-swimming planula stage and the nursing of the egg to the young polyp evidently serve a function in the life of the species: the need for larval settlement in a form immediately suited to hydroid life. Polyps were found by Louis AGASSIZ (1862, p. 243) in Massachusetts Bay to occur singly or in sparse aggregations in shore pools not exposed to strong wave action, and he thought that the species more properly belongs to deeper water. In England they have been found offshore near Plymouth, embedded in the sponge *Desmacidon fruticosum* (MONTAGU) (MARINE BIOLOGICAL ASSOCIATION U.K., 1957, p. 38). Little is known of the ecology of the hydroid, and the significance of the association with the sponge can only be conjectured. Probably the water currents maintained by the sponge are suited to the feeding requirements of the hydroid. The

paucity of larvae produced by each medusa is compensated for by the production of large numbers of medusae by each hydroid polyp and by the production from these medusae of abundant further medusae by budding. The nursing of the larvae, their release at an advanced stage of development and the production of large numbers of medusae are evidently aids to the avoidance of larval loss, to the dissemination of the species, and to affording the actinulae the best chance of finding suitable places for settlement.

The allied species *Tubularia indivisa* L. similarly nurses the eggs to actinulae within the bell-cavities of the gonophores. The gonophores are produced in large numbers on each polyp but are not released as free-swimming medusae. The actinulae are accordingly liberated in the vicinity of the parent polyps, and they tend to sink among the polyps and to settle on them. In this way large aggregate colonies develop. This must be of advantage to the species, ensuring that the hydroids form large aggregations in particular localities where water-currents and feeding are best suited to them.

Yet another allied species of Tubulariidae is of interest here. The medusa *Ectopleura dumortieri* VAN BENEDEN was found (WERNER and AURICH, 1955) to release its yolky eggs into the sea (instead of nursing them as in the two species we have just considered), the eggs there undergoing cleavage to form planktonic 'proactinulae', somewhat disc-shaped organisms with short rudiments of tentacles. The proactinula develops into a typical actinula, which, after several days of planktonic feeding, settles on the bottom and grows into the hydroid polyp. *Ectopleura dumortieri* is distributed in temperate and warm temperate seas of Europe and North America, and the medusae are found to occur, in British waters, in any month from March to December (RUSSELL, 1953, p. 78). The species is adapted to the long plankton season of these seas by the release of medusae over an extended period and by the planktonic feeding life of the actinulae. The polyps of *Ectopleura* are solitary, not aggregated as in *Tubularia*, and in this respect and in the release of medusae *Ectopleura* more resembles *Hybocodon*.

The somewhat different life-histories of *Hybocodon prolifer*, *Tubularia indivisa* and *Ectopleura dumortieri*, variants of a generally similar life-cycle, are not to be interpreted as indicating phylogenetic relationships within the Tubulariidae but as adaptations of these particular species to different conditions and different modes of life.

My next example of a species producing actinulae without a free planula stage is from the family Margelopsidae. Dr WERNER (1955) showed some years ago that the medusa *Margelopsis haeckeli* HARTLAUB, which occurs in shallow waters along the eastern coast of the North Sea, retains the developing eggs on its manubrium, where they develop into actinulae. These are released into the sea, where they become actinula-like mature hydroid polyps, which remain planktonic. These hydroids in turn produce medusae. The whole life-cycle is accordingly planktonic and is suited to the summer plankton conditions of these waters. (There is also a resting over-wintering phase in the life-history, to be mentioned later.)

In the family Myriothelidae, the large solitary hydroid *Arum cocksi* VIGURS, which is found attached to stones and rocks near low-water mark in Britain, has special stalked suckers which grasp the large eggs on liberation from the gonophores. The eggs there undergo development into actinulae, which are then released. The actinulae walk about on their tentacles for several days before settling down to become fixed polyps. There is no planktonic phase in the life-cycle, which is well adapted to the shore-living habit.

As is well known, in the oceanic Trachymedusae and Narcomedusae there is no bottom-living hydroid stage but development proceeds from the egg through a free-swimming ciliated planula stage to a swimming ciliated and tentaculate actinula, which transforms to the medusa. (The life-history in some Narcomedusae is complicated, but not essentially altered, by interpolation of a phase in the actinula stage when the actinula settles parasitically upon some medusa and undergoes vegetative production of numerous further actinulae, which transform to medusae.) BROOKS (1886) believed that the Trachylina are more primitive than the Leptolina and that the trachyline life-history throws light on the ancestry of the Hydroida. He advanced the theory (p. 411) that the remote ancestor of the hydromedusae was a solitary swimming actinula, with no medusa stage, and that this pelagic animal gradually became more and more highly organized and finally became converted into a medusa. I dispute this theory on two grounds. Firstly, the life-histories of modern trachyline medusae do not provide factual evidence for an ancestral life-cycle without a medusa stage. Secondly and more significantly, the Trachylina are oceanic deep-water animals specialized for that medium. I do not believe that the oceanic wholly pelagic mode of life is earlier than the shallow-water one. I consider that the oceanic habitat has been populated from shallow waters by forms that became specially adapted in structure and life-cycle for deep water. I explain the life-history of the Trachylina as having been modified from that of shallow-water hydromedusae by the limitation of the polyp stage to the actinula, which cannot settle (except, in some cases, parasitically on other pelagic animals) and accordingly transforms to the adult medusa.

We have seen that an actinula stage occurs in life-histories so diversified as those of Tubulariidae, Margelopsidae, Myriothelidae and Trachylina, and further examples could be adduced. This is not evidence for an actinula-like ancestor to the Hydroida. The actinula stage is merely the free-living first polyp developing after the gastrula stage. In very many species of Hydroida settlement and fixation occur before the first polyp forms, and accordingly in these species there is no free-living actinula. Where the first polyp is an actinula, this is an adaptation to the mode of life of the particular species.

In Corymorphine species, such as *Corymorpha nutans* M. SARS and *Euphysa aurata* FORBES, the medusae release large yolky eggs, which sink to the bottom, there undergoing cleavage to form non-motile gastrulae. The gastrula secretes a perisarcal envelope and becomes a plano-convex lenticular body attached by its flattened under-

side (REES, 1937; WERNER, 1959; EDWARDS, unpublished observations). There is no motile planula stage. The lenticular bodies are a specialized stage for settlement on the grains of sand or mud in the sediments in which the polyps live. At intervals varying from days to months young polyps hatch from these bodies and grow into the mature hydroid polyps. At the time of hatching the young polyps are equivalent to the actinulae of the species already discussed. The lenticular settlement bodies serve also as a resting stage in the life-cycle. The polyps do not emerge immediately but at variable intervals over a prolonged period. This extended period of hatching evidently has survival value for the species.

The medusa species *Margelopsis haeckeli* has already been mentioned because of the production of actinulae and planktonic hydroids in the summer. Dr WERNER (1955) further showed that the medusa produces two types of eggs. One type develops on the manubrium into an actinula, whereas the second type, after development to the gastrula stage, is released and sinks to the bottom, where it becomes an adherent plano-convex body enclosed in perisarc. These bodies serve as a resting stage in the life-cycle over the winter, hatching young polyps in the following spring to recommence the summer cycle. This species exhibits two kinds of life-cycle, one adapted to summer conditions, the other to winter.

We must briefly consider the significance of the gastrula stage. That it is an embryological stage of development of the organism, in which late cleavage and the formation of the primary tissue layers occur, is clear. In some species, such as those we have already considered, the gastrula is not ciliated but either transforms into an actinula or becomes an intermediate resting body, enclosed in perisarc, from which a young polyp is later hatched. In many species the gastrula is ciliated and motile, being known as the planula larva, and it eventually settles on some object, loses its cilia, secretes perisarc and becomes fixed, giving rise to a stolon and thence to the young attached hydroid colony. We know little of the conditions governing the choice of substratum for settlement by the planula, but it seems probable that the planula is guided by tactile and chemical sensory perception to a suitable substratum. Although much work has been carried out on the factors governing settlement of larvae of some other groups of marine animals, for example polychaetes, barnacles and polyzoans, limited work has been done on hydrozoan larval settlement. I have pleasure, however, in referring to the studies by Dr NISHIHIRA on the larval selection of algal substrates by epiphytic hydrozoans.

The ability of the Hydroida to reproduce vegetatively by budding is especially developed in the hydroid stage. Commonly the buds are not liberated but retain organic connection to form large colonies. This budding and colony formation and the production of special buds (gonophores) for sexual reproduction excited the interest of nineteenth century zoologists and led to the spate of discussion and long-continued debate on the so-called 'alternation of generations' or 'metagenesis'. I consider that the life-cycles of the Hydroida are, in essentials, very much like those of

other invertebrate animals with larval development. The so-called hydroid generation is a larval phase. The fact that hydroids commonly reproduce vegetatively is paralleled by vegetative reproduction of larvae in some other groups of animals, for example the Trematoda.

Even solitary polyps, such as *Corymorpha nutans*, *Euphysa aurata* and *Hydra* spp. reproduce vegetatively by buds. These buds, however, become free and colonies are not established. Indeed, the colonial form is unsuited to the specialized modes of life of these hydroids. The Corymorphine polyps live in sandy or muddy sediments, to which the solitary polyp form is best suited. *Hydra* species are active mobile animals, and a colonial form of polyp would be unsuited to this mode of life. In discussions of the phylogenies of hydroids there has been much debate as to whether solitary polyps originated from colonial forms, or the reverse. Since, as I have mentioned, solitary polyps undergo budding, the distinction between solitary and compound polyps is more apparent than real. Each life-form is a specialization for some particular habitat and mode of life. I consider that little of value can result from attempts to derive long-distant phylogenies from living species of Hydroida.

Budding is not confined to the hydroid stage. Some hydromedusae can multiply quickly by budding off further medusae and can thus take advantage of favourable plankton conditions for feeding and reproduction. They bud either from the manubrium (for example, *Sarsia gemmifera* FORBES, *Rathkea octopunctata* (M. SARS), *Lizzia blondina* FORBES) or from the tentacle bulbs (for example, *Sarsia prolifera* FORBES, *Hybocodon prolifer* L. AGASSIZ). The daughter medusae may in turn similarly bud off further medusae, and so on. A large population is soon built up. Eventually the resulting medusae reproduce sexually. In British waters *Hybocodon prolifer* and *Rathkea octopunctata* commonly produce large crops of medusae in spring in this way, and in summer *Lizzia blondina* may quickly appear in enormous numbers if conditions are suitable.

Another way of rapid production of medusae, found in a few species, is by fission of the medusae. For example, *Dipleurosoma typicum* BOECK undergoes transverse fission several successive times, the eventual daughter medusae becoming mature and reproducing sexually (EDWARDS, unpublished). This explains the erratic abundance of this species, which sometimes appears fairly suddenly in profusion. It also explains the great variability of form of the medusae.

Species of hydroids that do not release their gonophores as medusae are common, and I do not need to describe the modifications and specializations of structure, which are very well known to students of the Hydroida. The ability of these hydroids to reproduce sexually is interpreted as neotenic, that is the attainment of sexual maturity by an animal in its larval form. I am particularly concerned with the ecological significance of these cases. In the absence of a free medusa stage the species must rely on other means for dispersal. Two examples of dispersal by actinulae have been mentioned: *Tubularia indivisa* with briefly planktonic actinulae, and *Arum cocksi* with

actinulae that walk on rocky surfaces. In the majority of species, however, dispersal is achieved by their motile planulae. It is significant that very many of the hydroid species, especially thecate species, found in fairly shallow water and on the shore have no medusa stage. These hydroids are usually abundant and widely distributed, growing chiefly on rocks, stones, shells and weeds, and the planulae, which are assisted in their movements by water currents, are readily dispersed. Probably the planulae have a specialized behaviour ensuring that they find suitable places to settle. It seems likely that dispersal by medusae would be disadvantageous to species confined to the intertidal and immediately sublittoral zones. It is significant, too, that the many of thecate hydroids having no medusa stage have very profusely developed colonies. The number of feeding hydranths on these colonies is great and the gonophores are numerous, the production of planulae being accordingly very high. In contrast, those thecate hydroids that produce medusae, such as species of the families Laodiceidae and Mitrocomidae, have creeping and much less profusely developed colonies with far fewer hydranths. These species must rely to a considerable degree for their survival and dispersal upon the production of medusae, which have a moderately long planktonic life, during which they can drift considerable distances, attain large size and produce large numbers of eggs.

That the hydroid is a prolonged larval stage deserves special emphasis because it provides a long-term perennating phase in the life-cycle. In the course of my study of *Neoturris pileata* (FORSKÅL) in the Firth of Clyde (EDWARDS, 1965) I found that the medusae were in some years extremely abundant in ripe condition but that in many years, apparently because of unsuitable plankton conditions, the young medusae failed to grow to maturity. Because, however, of the profusion of its hydroid on the mollusc *Nucula* and because the hydroid is potentially capable of surviving as long as its molluscan host (many years) the survival of the species is not endangered by failure of the medusa crop, even in several successive years. Another case has come to my notice. The large leptomedusa *Staurophora mertensi* BRANDT, a species of cold water, is extremely rarely found in mature condition in the Firth of Clyde. Regular sampling of the plankton revealed, however, that the very young medusae occur in small numbers every year but rarely grow. The hydroid (a minute form not yet found there) must be persistent in the area for the species to survive there. As a corollary, a species may persist in the hydroid stage in an area unsuited to growth of viable medusae. For example, medusae of the species *S. mertensi* just mentioned, which are abundant around the Faroes and in other cold waters north of Scotland, are commonly drifted southwards along the east coasts of Scotland and England. Larvae produced by these medusae evidently settle along these coasts and establish the hydroid there, because young medusae newly liberated have been found as far south as the coast of Norfolk (HAMOND, 1957). These young medusae do not, however, grow up: the southern North Sea is unsuited to them, becoming too warm in spring and summer.

Hydroids are commonly associated with other animals, and it is instructive to

consider the ecological aspects of such relationships, especially the benefits to the hydroids. Many hydroids occur on other hydroids, deriving from them a foundation for settlement and growth and good conditions for catching food organisms. Bivalve molluscs commonly bear epizoic hydroids, which, in addition to finding the shell a suitable substratum for settlement, derive nutritional advantage from the water currents maintained by the molluscs. Very many gastropod molluscs support growth of hydroids, which benefit, in the collecting of food, from the movements of the hosts. I have also found that hydroids grow abundantly on and in the immediate vicinity of barnacles, and have concluded that the water currents maintained by the cirral action of the barnacles are of benefit to the hydroids in bringing food organisms to them. Other animals on which hydroids may be found include species of polychaete worms, decapod crustacea and shells inhabited by hermit-crabs: in all these associations the chief benefit to the hydroids is the facility for catching food.

In the course of a study of the life-cycle of the anthomedusa *Neoturris pileata* (FORSKÅL) I found that in the Firth of Clyde its hydroid occurs abundantly on molluscs of the genus *Nucula* but on no other animals (EDWARDS, 1965). Investigation of the ecological aspects of this association showed that the specific relationship between *Neoturris* and *Nucula* arises from adaptation of the hydroid to the particular mode of life of the molluscan host. *Nucula* moves above actively in the soft flocculent top layer of mud, where there are organisms for the hydroid to feed on and where the interstitial water is well oxygenated by the feeding and respiratory water-currents maintained by the mollusc. An individual *Nucula* that lives in a type of mud or at a depth in the mud unsuited to *Neoturris* bears no hydroid. No animals other than *Nucula* live in the type of mud and have the habits suited to *Neoturris*.

In contrast to the above association, the related hydroid *Leuckartiara octona* (FLEMING) is found commonly on a wide variety of animals that live on the surface of mud: many gastropod and pelecypod molluscs, crabs, the polychaete worm *Aphrodite aculeata* L., and other animals. This hydroid has an erect and branching form, and it is adapted not for life within the mud but for living on and just above the surface. It is accordingly able to live on various hosts.

We do not know whether planulae have a specific behaviour for finding and settling on suitable hosts, though it is extremely likely that they have. An observation I made when rearing the hydroid *Podocoryne borealis* (MAYER) suggests that planulae probably defer attachment until they have found a suitable substratum. In nature this hydroid is found on various mobile animals that live on muddy grounds (EDWARDS, 1972), but it is sometimes found on stones and rocks. I noticed that in my glass culture bowls the planulae when fully developed spent several days loosely attached by one end. When disturbed by agitation of the water they energetically twisted about, as presumably they would do if stimulated by some active animal. However, in my bowls they eventually became attached to the glass and developed into colonies. It is probable that in nature large numbers of planulae are wasted because they fail to

find suitable hosts, or because they happen to settle on hosts that do not live on a type of ground suited to the hydroids or behave in a manner unsuited to the hydroids.

I wish to consider briefly the solitary Corymorphine hydroids *Corymorpha nutans* and *Euphysa aurata*, because they and related species have entered much into discussions of the phylogeny of hydroids. The small polyp *Euphysa aurata* lives in fine muddy sediments, for which it is adapted by a loose perisarcal envelope with a few root-like attachment processes. The very extensile moniliform aboral tentacles are spread above the mud and serve as efficient fishing lines. The erect very much larger *Corymorpha nutans* lives in sandy sediments of coarser grain than the muds favoured by *Euphysa*. It has very numerous rooting filaments for anchorage and support. The large stem is supported by endodermal parenchymatous tissue, the stem-cavity taking the form of a number of slender longitudinal branching and anastomosing canals in the peripheral part of the endoderm. The large head has a whorl of numerous filiform aboral tentacles, displayed for catching planktonic organisms. Within the head there is a parenchymatous diaphragm, which, among other possible functions, evidently serves as mechanical support for the large head with its numerous long tentacles and its long branched blastostyles loaded with gonophores. (Both *Euphysa* and *Corymorpha* have oral tentacles around their distal extremities.) The differences in size and complexity of structure between these two hydroids have by some workers been construed as evidence for evolution within the Corymorphidae. REES (1957), for instance, in his well-known paper on evolutionary trends in capitate hydroids and medusae, thought that *Euphysa aurata* is simpler and more primitive, because of its smaller size, moniliform aboral tentacles and lack of a gastric diaphragm, than the large and more complex, *Corymorpha nutans*, which he regarded as "higher'. He considered the moniliform type of tentacle to be primitive compared with the filiform, but he encountered difficulty in explaining the presence of moniliform tentacles in the medusae of both species. In this and other cases his theory persistently ran into trouble in the course of his argument, especially because of contradictions within the same or allied species arising from the presence of what he regarded as 'primitive' and 'advanced' characters. The differences between *Euphysa* and *Corymorpha* polyps do not, in my estimation, prove or suggest anything about phylogenetic relationships. They are specialized adaptations to different modes of life, and do not justify us in regarding either species as being more primitive or more advanced than the other. It is significant that the medusa of these two species have similar habits, both have moniliform tentacles and do not differ from each other in essentials of structure.

I have not the time in this paper to discuss further the theories that attempt to derive phylogenies in the Hydroida from the structure and life-histories of living species, nor do I think such attempts meaningful. The characters that we find in modern species are not to be interpreted as 'primitive' or 'simple' or 'advanced', but to be regarded as serving specialized functions in the present life-processes of these species. This emphasizes the necessity for a full study and a proper understanding

of the life functions of hydroids and medusae. There has, in recent years, been a most welcome and necessary advance in knowledge of whole life-cycles of species of Hydroida, but very much remains to be done. The hydroids of a high proportion of the known medusae of the world still await discovery, and, on the other hand, little is known of the biology of the great number of described species of hydroids, which, for the most part, have been studied only as preserved museum specimens. Notwithstanding these gaps, it is very necessary that a single unified classification and nomenclature of hydroids and medusae be adopted. Nomenclatorial problems that arise in achieving this can be overcome by use of the International Code of Zoological Nomenclature and by reasonable application of good taxonomic practice.

Taxonomic considerations apart, there is a rich harvest to be gathered in the study of the habits and functions of hydroids and medusae and of their specialized adaptations for particular modes of life. The physio-ecological approach to the study of these animals has increasingly become adopted by modern workers, and a great new field of investigation opens up.

Summary

Because of the way in which, historically, our knowledge of Hydroida has been built up, by workers who have often specialized in the study of either hydroids or medusae, there grew up two systems of classification and nomenclature, one for hydroids and another for hydromedusae. The need for rectifying this has long been appreciated, but achievement of a unified system has been delayed by deficient knowledge of the life-cycles of the species. There has, however, been much success in recent years in working out their life-histories, and we now have sufficient information to be able to attempt a single taxonomic and nomenclatorial system for the Hydroida. It is very desirable that the life-histories and biology of the large number of species of hydroids and medusae described from many parts of the world be studied.

There has long been an interest in the evolution and phylogenies of the Hydrozoa and debate on the evolutionary significance of the hydroid and medusa stages. It is considered that extremely early in the history of the group a basic life-history was established involving development from the egg through blastula and gastrula stages to a tentaculate polypoid larva (hydroid stage) and thence to the muscular swimming abult. All the variant life-histories of modern species can be explained as specializations and modifications to meet ecological and physiological needs of the particular species. Examples are given to illustrate this.

The importance, too, of the hydroid as a prolonged larval stage providing a long-term perennating phase in the life-cycle is emphasized.

Ecological aspects of associations between hydroids and other animals are considered.

Characters found in modern species are not to be interpreted as 'primitive' or

'simple' or 'advanced' but to be regarded as serving specialized functions in the present life processes of these species. Attempts to derive phylogenies in the Hydroida from living species are regarded as of very doubtful validity.

The necessity for a full study and a proper understanding of the life functions of hydroids and medusae is emphasized. Despite the important advances in recent years in our knowledge of life-histories, little is known of the biology of the majority of the great number of species described. There is a rich field for investigation in the study of the habits and functions of hydroids and medusae and of their specialized adaptations for particular modes of life.

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DISCUSSION

MACKIE: The reduction of the medusa stage in many life-cycles, which often goes along with a short planktonic larval stage, suggests that there may be little need for a dispersal stage as such. Where the species is established in a suitable, stable location, the life cycle is geared toward *avoidance* of dispersal (e.g. *Tubularia*). Why then are medusae retained in so many life cycles? Perhaps it is chiefly because the medusae have access to the productive upper layers of the water. They would then serve chiefly as a trophic stage, and because the gonads have a high energetic requirement, they would normally be borne by the medusae. By this argument the hydroid exists to repopulate coastal waters seasonally, as the medusae tend to be lost by dispersion, winter starvation, etc. Would you agree that we should stop talking about the medusae as a "dispersal phase" as though this were an advantage stage conferred on the life cycle? In fact it must often be a disadvantage but one which is inseparable from the trophic advantages gained by becoming pelagic.

EDWARDS: I agree that the medusa is a trophic phase, taking advantage of the rich plankton at suitable seasons. The medusa, which is often long-lived and may be drifted considerable distances, is however an important phase in dissemination of the species. In the cases of species without medusae, such as many shallow-water hydroids, the ciliated planulae serve for disseminating the species, in which they are assisted by water-movements. In all species the hydroid is a perennating trophic phase.